SYNOPSIS OF A NEW NEOTROPICAL HAIRSTREAK GENUS, *JANTHECLA*, AND DESCRIPTION OF A NEW SPECIES (LYCAENIDAE)

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ABSTRACT. We describe *Janthecla* Robbins and Venables in the Eumaeini with *Thecla janthina* Hewitson as type, transfer eight additional neotropical species from *Thecla* Fabricius to *Janthecla*, and name a new species, *J. leea* Venables & Robbins. The new species had been misidentified as *T. janthina*, but the two are sympatric in northern Venezuela. We give distribution, habitat, and distinguishing traits for each *Janthecla* species and present an identification key to males. New synonymies are *J. janthina* (Hewitson) = *J. venezuelae* (Lathy) and *J. rocena* (Hewitson) = *J. major* (Lathy); *J. janthodonia* (Dyar) is removed from the synonymy of *J. janthina*. We code 12 characters, from which we infer phylogenetic relationships among *Janthecla* species.

Additional key words: Theclinae, Eumaeini, androconia, cladogram, comparative morphology.

The current taxonomy of *Thecla janthina* Hewitson (Theclinae) is incorrect. Draudt (1921-22) recorded *T. janthina* from Guatemala to Brazil, but individuals from South America east of the Andes belong to an undescribed species that is sympatric with *T. janthina* in northern Venezuela. Similarly, *T. janthina* and *T. janthodonia* Dyar have been considered conspecific (Hoffmann 1940), but are distinct and sympatric. Lastly, *T. venezuelae* Lathy, which was described as a subspecies of *T. janthina*, is a synonym of *T. janthina*.

The original purpose of this paper was to correct the nomenclature for *T. janthina* and to describe the South American species that had been confused with it. However, we could not place the *T. janthina* complex in an existing eumaeine genus—*Thecla* Fabricius belongs to the Theclini, not the Eumaeini (Eliot 1973). In the process of determining those eumaeines that are closely related to *T. janthina*, we discovered enough information to expand upon our original purpose. Thus, in this paper, we (1) describe a new genus, *Janthecla*, for *T. janthina* and relatives, (2) name the new species that had been confused with *T. janthina*, (3) discuss the species that belong to *Janthecla*, with notes on their distribution, morphology (emphasizing androconia), and biology, (4) present an identification key to males, and (5) propose a preliminary cladogram of phylogenetic relationships among these species. A secondary reason for expanding the paper is that it allows us to assess the phylogenetic position of T. rocena Hewitson, a species that had been reported to have an aberrant male foreleg (Robbins 1987).

Abbreviations for museum collections are as follows: AME-Allyn Museum of Entomology, Sarasota; AMNH-American Museum of Natural History, New York; BMNH-The Natural History Museum (formerly British Museum), London; CMNH-Carnegie Museum of Natural History, Pittsburgh; MIZA-Instituto de Zoologia Agricola, Maracay; NMNH-National Museum of Natural History, Washington; MUSM-Museo de Historia Natural Universidad Nacional Mayor de San Marcos, Lima; and UFPC-Universidade Federal do Parana, Curitiba. Abbreviations for private collections are: CVC-Charles V. Covell Ir., Louisville, Kentucky, USA; JBS-J. Bolling Sullivan, Beaufort, North Carolina, USA; ROM-Romero family, Maracay, Venezuela.

Janthecla Robbins & Venables, new genus

Type species. Thecla janthina Hewitson 1867.

Systematic placement. Janthecla belongs to the Eumaeini (Lycaenidae: Theclinae) as characterized by Eliot (1973). It has ten forewing veins (Fig. 22), hairy eyes, a stubbytipped male foreleg tarsus (Fig. 21), and "greyhound-shaped" male genitalia lacking a juxta (Figs. 23–26). The closest relatives of *Janthecla* within the Eumaeini are unknown. We discuss interspecific morphological variation in the Comparative Morphology section below.

Unique character state. The cervix of the female genitalia characterizes Janthecla. Attachment of the corpus bursae to the ductus bursae is more posterior ventrally than dorsally (Figs. 27-29). However, in J. malvina the anterior ductus bursae is sharply curved so that the points of attachment are ventral and dorsal (Fig. 28), rather than posterior and anterior. This cervical morphology has not been reported previously in the Eumaeini and appears to be unique.

Field identification. A conspicuous submarginal green spot in ventral hindwing cell Cu2-2A (Figs. 2, 4, 8, 9) coupled with either two ventral forewing white lines or a single disjoint white line distinguish Janthecla from all other eumaeines. Because the genus contains two ventral wing patterns, that typified by J. leea (Figs. 2, 4) and that of J. rocena (Figs. 8, 9), learning these two patterns is an easy means of field identification.

Specific identification. Most Janthecla species are not easy to identify. Males are distinguished by presence or absence of a dorsal forewing scent patch, and when present, its shape and placement. For this reason, we emphasize description and illustration (Figs. 12-20) of these patches. Other useful distinguishing characters are presented in the identification key. Although we examined antennae, labial palps, wing patterns, and abdomens, including genitalia, we cannot distinguish females of some sympatric species.

Biology. Janthecla species occur most often in wet (> 200 cm annual precipitation) lowland forests (they are uncommon above 1000 m) except that *I. flosculus* apparently is not found in the lowlands. Males of J. rocena are territorial in the mid-afternoon. No larval foodplants are recorded for the genus.

Etymology. Janthecla is an arbitrary combination of "janthina" and "Thecla." Its gender is feminine.

Key to Males

Without a red spot at base of the ventral hindwing

^{...2}

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2	2. Dorsal forewing without androconia 3 - Dorsal forewing with androconia 4
-	- Dorsal forewing with androconia4
3	B. Forewing costa tan J. janthodonia Forewing costa white J. leea
_	- Forewing costa white I. leea
4	4. Dorsal forewing cell Cu2-2A black, without iridescent blue scales (Fig. 18)
	J. cydonia
	- Dorsal forewing cell Cu2-2A with black and iridescent blue scales5
5	5. With a small "v-shaped" scent patch along the bases of dorsal forewing veins M1
	and Cu1 (Fig. 16) J. janthina
-	- Without a small "v-shaped" scent patch along the bases of dorsal forewing veins
	M1 and Cu16
6	M1 and Cu16 5. Dorsal forewing scent patch does not cover vein ldc (Fig. 12) <i>J. malvina</i>
-	- Dorsal forewing scent patch does cover vein ldc (Figs. 13-15, 20)7
7	7. Dorsal forewing scent patch small (<3 mm across) (Figs. 13, 20)8
-	- Dorsal forewing scent patch large (>3 mm across) (Figs. 14, 15) 9
8	B. Dorsal forewing scent patch centered on base of wing cell M3-Cu1 (Fig. 20)
	J. armilla
-	- Dorsal forewing scent patch centered on veins mdc and ldc (Fig. 13) J. flosculus
	9. Ventral cornutus wide (>0.16 mm). Coastal Brazil from Bahia to Santa Catarina
	and Misiones, Argentina J. aurora
-	- Ventral cornutus narrow (<0.16 mm). Guianas, Orinoco and Amazon Basins
	J. sista

Note: The forewing of *J. sista* is more falcate than that of *J. aurora* (see Comparative Morphology section), its scent pad is usually larger, and its apical border is wider on average, but width of the ventral cornutus is the most definitive character for separating these two species.

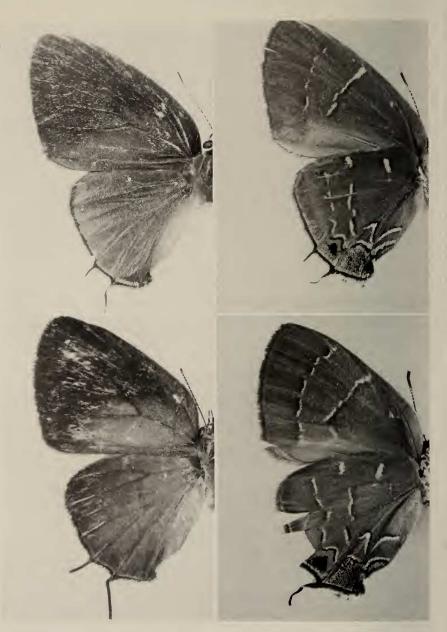
SYNOPSIS OF SPECIES

We use Comstock and Huntington (1959-64) and Bridges (1988) as nomenclatural references. They contain citations to original descriptions. Synonymies and combinations not noted in these works are designated as new.

1. Janthecla rocena (Hewitson 1867), new combination (Figs. 5, 8, 9, 21, 23, 27)

= Janthecla major (Lathy 1926). NEW SYNONYMY

Male forewing length: 17.2 mm (s = 1.44, n = 89). Distribution (Fig. 5): Mexico (Chiapas) to southern Brazil (Parana), but not recorded from coastal Brazil. The type locality is the Amazon. Habitat: Wet lowlands to 1100 m. Biology: Robbins (unpubl.) observed territorial males landing 2–3 m high in a sunlit area along a trail through late secondary forest on Barro Colorado Island (Canal Area, Panama) on 24 and 25 July 1977 at 1430–1530 hours. Geographical variation: Three specimens from the southern extreme of the range (Parana, Brazil) differ from the others. Their dorsal wing borders are narrower. The ventral forewing submarginal white line, which is absent in other specimens of J. rocena is represented by a few spots (Figs. 8, 9). Since there are not enough specimens from intermediate areas with which to assess geographical variation, we cannot rule out the possibility that the Parana specimens represent a distinct species. Their genitalia, however, are indistinguishable from those of J. rocena elsewhere. Identification: Both sexes are distinguishable from these of the ventral hindwing. Androconia: A cluster of black androconia occurs along the inner margin of the ventral forewing (Fig. 8). Nomenclature: Lathy (1926) differentiated Thecla major (type locality: Muzo, Co-



FIGS. 1-4. Janthecla leea. 1, Upperside male (Peru). 2, Underside male. 3, Upperside female (Venezuela). 4, Underside female.

lumbia) from *T. rocena* by wing pattern characters (size, extent of dorsal blue, underside color and markings) that vary similarly in all populations. **Other illustrations:** Adults (De La Maza 1987 as "*Thecla*" *minyia*), legs (Fig. 21), and genitalia (Figs. 23, 27). **Material examined:** 52 males and 4 females.



FIG. 5. Distribution of J. rocena (circles) and J. malvina (triangles).

2. Janthecla malvina (Hewitson 1867), new combination (Figs. 5, 12, 24, 28)

Male forewing length: 15.2 mm (s = 1.04, n = 8). Distribution (Fig. 5): Guianas, Amazon Basin, and coastal Brazil. The type locality is Rio de Janeiro, Brazil. Habitat: Lowlands to 700 m. Identification: Both sexes can be distinguished from other Janthecla by their more inclined postmedian line on the ventral forewing. This species and J. armilla are the rarest Janthecla species in collections. Androconia: A somewhat oval cluster of gray-brown androconia occurs at the upper end of the dorsal forewing discal



FIG. 6. Distribution of *J. janthodonia* (circles), *J. cydonia* (solid triangles), *J. leea* (squares), and *J. armilla* (hollow triangles).

cell (Fig. 12). Other illustrations: Adults (Lewis 1973 as *Thecla malvina*) and genitalia (Figs. 24, 28). Material examined: 13 males and 5 females.

3. Janthecla janthodonia (Dyar 1918), new combination (Figs. 6, 17)

Male forewing length: 15.3 mm (s = 0.47, n = 8). Distribution (Fig. 6): Mexico (San Luis Potosi, Veracruz, Tabasco, Chiapas) and eastern Guatemala (Izabal). The type locality

is Santa Rosa, Veracruz, Mexico. Habitat: Lowland forest. Identification: Hoffmann (1940) treated this taxon as a subspecies of *J. janthina*, but it differs by its lack of androconia, narrower ventral cornutus, lack of white scales on the forewing costal margin, lack of iridescent blue in the dorsal forewing discal cell, and darker dorsal forewing blue color. **Possible hybrid:** There is a Mexican male (Veracruz, Presidio) from the Hoffmann collection (AMNH) that we believe to be a hybrid between *J. janthodonia* and *J. janthina* and that may account for Hoffmann's failure to recognize these two taxa as distinct. This specimen has the dorsal blue color and ventral cornutus of *J. janthina*, but lacks white scales on the forewing costal margin, as in *J. janthodonia*. The part of the forewing discal cell that is blue in *J. janthina* and black in *J. janthodonia* is a mixture of blue and black scales. Where *J. janthina* has a scent patch, there are black scales shaped like regular wing scales, not reduced in size like the androconia of *J. janthina*. Androconia: None (Fig. 17). Nomenclature: Comstock and Huntington (1959–64) incorrectly gave 1919 as the date of publication. Material examined: 17 males and 5 females.

4. Janthecla cydonia (Druce 1890), new combination (Figs. 6, 18)

Male forewing length: 15.0 mm (s = 1.03, n = 8). Distribution (Fig. 6): Costa Rica to northern Colombia (Magdalena) and western Ecuador (Pichincha). The type locality is the interior of Colombia. Habitat: Wet forest from sea level to about 700 m. Identification: Males are immediately recognizable by their almost all black dorsal forewings, but we cannot distinguish females from those of sympatric J. *janthina*. Androconia: A narrow band of iridescent gray or blue (depending upon the angle at which they are viewed) androconia occurs at the end of the dorsal forewing discal cell over veins mdc and ldc (Fig. 18). Material examined: 31 males. Also, 15 females that may be this species.

5. Janthecla leea Venables & Robbins, new species (Figs. 1–4, 6, 19, 22, 26, 29)

Male forewing length: 14.4 mm (s = 0.56, n = 8). Distribution (Fig. 6): Northern Venezuela, the Guianas, and the Amazon Basin. Habitat: Wet forest to 1100 m. Identification and distinguishing characters: Janthecla leea has been misidentified as J. janthina (Draudt 1921-22). Male J. janthina have a scent patch at the base of dorsal forewing veins M3 and Cu1 whereas male J. leea lack androconia (Figs. 16, 19). Where J. janthina and J. leea are sympatric in Henry Pittier National Park (Aragua, Venezuela), the hindwings of both sexes of J. janthina have translucent patches that are lacking in J. leea (Figs. 1, 3, 11). The lack of androconia differentiates male J. leea from other Janthecla species except J. janthodonia, whose forewing costa lacks white scales. Also, the ventral cornutus of J. leea is significantly wider (Table 3) than that of J. janthodonia (t = 3.910, df = 14, P < 0.01). We cannot distinguish females of J. leea from those of sympatric J. sista. Androconia: None (Fig. 19). Other illustrations: Adults (Figs. 1-4), wing venation (Fig. 22), and genitalia (Figs. 26, 29).

Holotype. The holotype is a male labelled "PERU, 20 km SW Pto. Maldonado, 25 Oct. '83, S. S. Nicolay." We added a red label—"Holotype, *Janthecla leea* Venables and Robbins." The specimen is in excellent condition except that the left antenna is broken. It is deposited in NMNH. The locality is about 10 km from the Tambopata Reserve and is called Infierno by the local inhabitants.

Paratypes. We designate 48 male and 2 female paratypes and have labelled all except for 4 individuals for which we mailed the paratype labels, as noted. We cannot distinguish females of *J. leea* from those of *J. sista*, but can from females of *J. janthina* (as noted above) and thus recognize only two female paratypes from northern Venezuela, where *J. sista* does not occur. VENEZUELA: Aragua, Rancho Grande 1 ô, 1 ° (NMNH), 1 ô, 1 ° (MIZA, paratype labels sent), 2 ô (ROM, Maracay, paratype labels sent), 1 ô (JBS). GUYANA: Potaro River 1 ô (AME). FRENCH GUIANA: St. Jean, Maroni 2 ô (NMNH). COLOMBIA: Meta, Rio Ariari 1 ô (NMNH), Villavicencio 1 ô (AME); Vaupes, Mitu 1 ô (NMNH); Amazonas, Leticia 1 ô (CVC), Napo, Rio Tiputine 1 ô (JBS). PERU: Madre



FIG. 7. Distribution of *J. janthina* (hollow triangles), *J. sista* (squares), *J. aurora* (solid triangles), and *J. flosculus* (circles).

de Dios, 30 km SW Pto. Maldonado = Boca Rio La Torre = Tambopata 3 ô, 4 ô (MUSM), 2 ô (CVC); Huanuco, Tingo Maria 1 ô (NMNH); Loreto, Yanamono, 80 km E Iquitos 1 ô (MUSM), Iquitos 1 ô (AME); San Martin, Bonilla, Km 75 Tarapoto-Yurimaguas 1 ô (MUSM). BOLIVIA: Cochabamba, Chapare 1 ô (NMNH); Santa Cruz, 17°46–55'S Lat. 63°5–34' Long. 2 ô (NMNH), Buena Vista 1 ô (CMNH), Rio Surutu 1 ô (CMNH). BRAZIL: Para, Belem 1 ô (AME), Obidos 1 ô (AME); Amazonas, 75–85 km N Manaus 1 ô (UFPC), Dist. Agr. da Suframa 1 ô (JBS), Manaus 2 ô (AME), Mancapuru 13 ô (CMNH), S. Paulo de Olivenca 1 & (NMNH); Rondonia, Ariquemas 2 & (NMNH); Mato Grosso, Diamantino, Alto Rio Arinos 1 & (NMNH), 1 & (UFPC); Goias, Tower, 10 km N Goiania 1 & (NMNH).

Etymology. In Middle English, "lee" means "a calm and sheltered place." It is also the first name of Lee Venables, an avid entomologist who has provided support during this project. We consider "leea" to be an indeclinable, non-latinized name.

6. Janthecla armilla (Druce 1907), new combination (Figs. 6, 20)

Male forewing length: 14.4 mm (s = 1.17, n = 8). Distribution (Fig. 6): Coastal Brazil from Minas Gerais and Espirito Santo to Santa Catarina. The type locality is Rio de Janeiro, Brazil. Habitat: Lowlands. Identification: We cannot distinguish females of J. armilla from those of J. aurora, but males can be separated by the wider dorsal forewing border of J. armilla as well as by the smaller scent patch. Androconia: Iridescent scales are mostly covered by regular blue wing scales, such that the scent patch appears to change when viewed at different angles. The androconia cover dorsal forewing vein ldc and the basal end of cell M3-Cu1 (Fig. 20). Material examined: 9 males. Also, 7 females that may be this species.

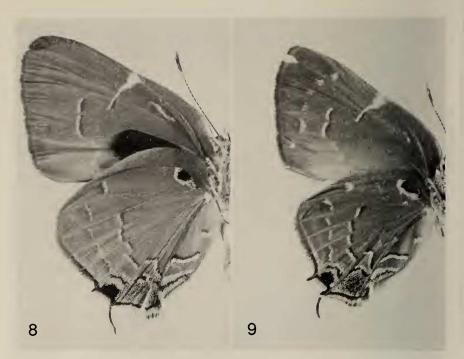
7. Janthecla janthina (Hewitson 1867), new combination (Figs. 7, 10, 11, 16, 21, 25)

= Janthecla venezuelae (Lathy 1930). NEW SYNONYMY

Male forewing length: 15.1 mm (s = 1.25, n = 8). Distribution (Fig. 7): Mexico (Veracruz) to western Ecuador (Pichincha) and east to northern Venezuela (Aragua). The type locality is Vera Paz, Guatemala. Habitat: Wet forest from sea level to 1250 m. In Panama, individuals fly in small clearings and edges of late secondary forest, often in the shade. Geographical variation: Scale density in the basal half of the hindwing is lowerso that the hindwing appears translucent—in both sexes from northern Venezuela than in those from Central America (Figs. 10, 11), but individuals from northern and western Colombia (Santander, Caldas, Valle, Choco) are phenotypically intermediate, as noted by Lathy (1930), indicating that this variation is clinal. Identification: Both sexes have white scales on the forewing costal margin whereas these white scales are lacking in *I*. janthodonia. Where J. janthina and J. leea overlap in northern Venezuela, both sexes can be distinguished by the translucent patch at the base of the hindwing in J. janthina. We cannot distinguish females of J. janthina and J. cydonia. Androconia: The scent patch is composed of small iridescent scales, similar to those in J. armilla, but restricted to the base of dorsal forewing veins M3 and Cu1 (Fig. 16). Nomenclature: The type series of Lathy's (1930) *Thecla venezuelae* includes several Venezuelan specimens in the BMNH, "others" in the NMNH (actually one Venezuelan specimen), and a male in the Fournier Collection in Paris of unknown locality. This taxon represents the translucent phenotype. Since it is a clinal geographical form of J. janthina, as noted by Lathy, it is a synonym. Other illustrations: Legs (Fig. 21) and genitalia (Fig. 25). Material examined: 54 males and 3 females. Also, 15 females that may be this species.

8. Janthecla sista (Hewitson 1867), new combination (Figs. 7, 14)

Male forewing length: 13.5 mm (s = 0.67, n = 8). **Distribution** (Fig. 7): Guianas, eastern Venezuela, and Amazon Basin. The type locality is the Amazon (mistakenly listed as Mexico in Bridges 1988). **Habitat:** Wet forest from sea level to about 1000 m (eastern slope of the Andes). **Identification:** Generally the most common *Janthecla* species where it occurs. We are unable to distinguish females of *J. sista* from sympatric females of *J. leea*. **Androconia:** The scent patch is complex. There is a large patch of brown or gray scales covering the distal half of the dorsal forewing discal cell and the area beyond the

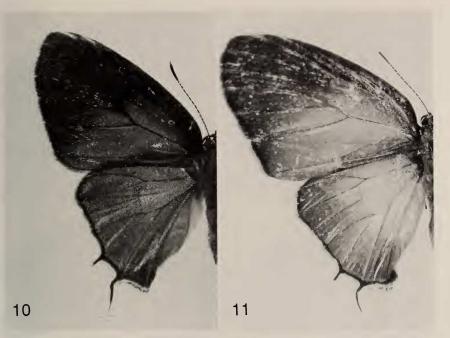


FIGS. 8, 9. Underside of *J. rocena* showing geographical variation in presence of forewing submarginal row of white dots. 8, Male from Panama without white dots. 9, Female from Brazil (Parana) with white dots.

discal cell to the wing border. The wing veins in this patch are covered with small iridescent gray-blue-green scales, similar to those in *J. janthina* (Fig. 14). Material examined: 164 males. Also, 22 females that may be this species.

9. Janthecla aurora (Druce 1907), new combination (Figs. 7, 15)

Male forewing length: 14.3 mm (s = 0.95, n = 8). Distribution (Fig. 7): Coastal Brazil (Bahia to Santa Catarina and Rio Grande do Sul—Druce 1907), west to Argentina (Misiones). The type localities are Espiritu [sic] Santo and Rio Grande, Brazil. Habitat: Lowland forest up to 800 m. Geographical variation: The dorsal forewing scent patch of males is separated from the distal black border by blue scaling in specimens from Santa Catarina (Brazil), but this trait is variable in individuals from Bahia, Minas Gerais, and Espirito Santo. The extent of white scales on the forewing costa is often reduced in specimens from Rio de Janeiro and south. Identification: We are unable to distinguish females of J. aurora from sympatric females of J. armilla. Androconia: The scent patch is the same as in J. sista except slightly smaller (Fig. 15). Material examined: 37 males. Also, 7 females that may be this species.



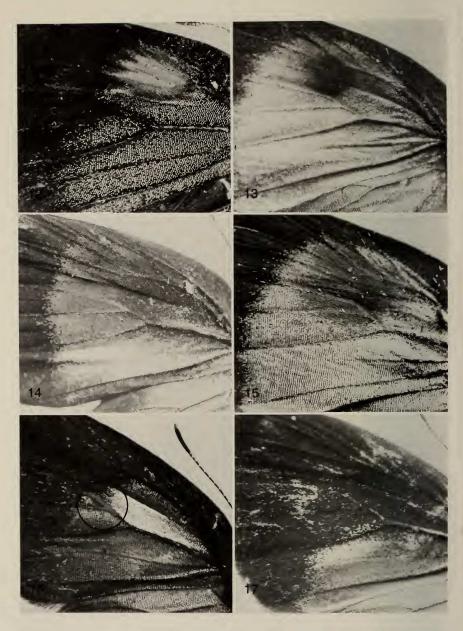
FIGS. 10, 11. Upperside of *J. janthina* showing geographical variation. 10, Male from Panama. 11, Male from northern Colombia (Victoria, Caldas) with translucent patches.

10. Janthecla flosculus (Druce 1907), new combination (Figs. 7, 13)

Male forewing length: 14.1 mm (s = 0.70, n = 8). Distribution (Fig. 7): Espirito Santo to Santa Catarina (Brazil). The type locality is Espiritu [sic] Santo, Brazil. Habitat: Coastal mountains, usually above 500 m, possibly restricted to moist forests. It is not known from lowlands and does not appear to be sympatric with *J. aurora*. Identification: Both sexes are distinguished from *J. aurora* and *J. armtlla* by a lack of white scales on the forewing costal margin. Androconia: A cluster of small iridescent gray-green scales covering the distal end of the dorsal forewing discal cell and extending beyond the discal cell between veins R3 and M3 (Fig. 13). Material examined: 12 males and 3 females.

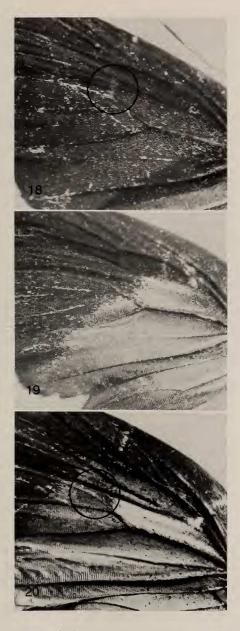
COMPARATIVE MORPHOLOGY

We describe and code characters in *Janthecla* and summarize character state distributions in Table 1. We use a dash to indicate situations in which information is lacking. The remainder of the Eumaeini is our outgroup because we have not been able to narrow the outgroup to a portion of the tribe. For characters in which each of the states occurs in other eumaeines, we code the outgroup with a dash and usually list two representative eumaeine taxa with each state.



FIGS. 12-17. Upperside male forewing showing androconial cluster (circled). 12, J. malvina. 13, J. flosculus. 14, J. sista. 15, J. aurora. 16, J. janthina. 17, J. janthodonia.

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FIGS. 18–20. Upperside male forewing showing androconial cluster (circled). 18, J. cydonia. 19, J. leea. 20, J. armilla.

	Characters											
Taxon	1	2	3	4	5	6	7	8	9	10	11	12
J. rocena	1	1	2	0	0	0	1	0	0		1	0
J. malvina	0	0	2	1	1	1	1	1	1		1	1
J. janthodonia	0	0	3	1	1	1	0	0	2	0	1	1
J. cydonia	0	0	3	1	1	1	0	0	2	1	1	1
J. leea	0	0	3	1	1	1	0	0	2	1	1	1
J. armilla	0	0	1	1	1	1	0	0	2	1	1	1
J. janthina	0	0	3	1	1	1	0	0	2	1	1	1
J. sista	0	0	2	1	1	1	0	0	2	1	1	1
J. aurora	0	0	1	1	1	1	0	0	2	2	1	1
J. flosculus	0	0	0	1	1	1	0	0	2	2	1	1
Other Eumaeini	0	0			-	0		0	—	—	0	0

TABLE 1. Data matrix for *Janthecla*. Characters and their states are discussed in text. A dash means that information is missing or ambiguous.

Antennae. The antennae of *Janthecla* are comprised of 29–36 segments. The nudum occurs on the last 12–16 segments and is confined to the club in both sexes. There is little interspecific variation except that the average number of segments in *J. rocena* is about 2 more than the other species.

Legs. The unusual male foreleg of *J. rocena* differs from other lycaenids (Robbins 1988) (Fig. 21). The coxa and femur are elongated while the tibia is shortened. The distal femur is bulbous, and the inner surface of it and the tibia have a scale brush (not evident in the figure). The scale brush may be rubbed against the ventral forewing androconia and used during courtship.

Character 1. Length of male foreleg femur (0) shorter than length of tibia plus tarsus (Fig. 21), (1) longer than length of tibia plus tarsus (Fig. 21). Comment: Among the Eumaeini, character state 1 is restricted to *J. rocena*.

Character 2. Male foreleg femur (0) without a scale brush, (1) with a scale brush. Comment: Although some pierids have a scale brush on the foreleg tibia (Robbins 1990), the brush on the foreleg femur in *J. rocena* is unique among the Papilionoidea.

Wing venation, shape, and pattern. The wing venation of J. leea (Fig. 22) is typical of the genus. However, male forewing shape varies markedly in the degree to which the apex is produced, and we quantified this variation. All species except J. rocena share the same ventral wing pattern. Whether the forewing costa is white or tan varies within the genus, but we did not code it because it is geographically variable within J. aurora.

Character 3. Ratio of the length of male forewing vein 2A divided by length from the base of vein 2A to the forewing apex (0) >0.827, (1) <0.827 and >0.803, (2) <0.803 and >0.759, (3) <0.759 (see Table 2 for means and standard deviations). Comment: We measured these distances under a microscope at $15 \times$ using a digitizing



FIG. 21. Male forelegs of *J. rocena* (right) and *J. janthina* from Panama. The tarsus is at bottom and coxa at top.

pad and calculated a *t*-statistic between pairs of means on arcsine transformed ratios (Sokal & Rohlf 1969). We then assigned means to different character states (Table 2) if the distance between them was "significant" at the 0.05 level using a 2-tailed *t*-test. Because we chose pairs a posteriori, this gap criterion does not mean that the differences were significant in the usual statistical sense. Rather, we simply used this difference as a gap criterion. Farris (1990) is a recent reference that provides citations to the literature on coding continuously varying characters. Among other eumaeines, male forewing shape varies from *Pseudolycaena* Wallengren, with falcate wings, to *Trichonis* Hewitson, with almost rectangular wings (Robbins 1987).

Character 4. Base of ventral hindwing (0) with a red spot (Figs. 8, 9), (1) with no red scales (Figs. 2, 4). Comment: Character state (0) occurs in eumaeines such as *Atlides inachus* (Cramer) and *Olynthus narbal* (Stoll) (Nicolay 1982) and state (1) in *Arcas imperialis* (Cramer) (Nicolay 1971b) and *Symbiopsis lenitas* (Druce) (Nicolay 1971a).

Androconia. Robbins (1991) differentiated scent pads (androconia underlain by a chamber between the wing membranes, see Thomas 1893 for histology) from scent patches, which lack the chamber. We dissected the wings of *J. janthina* and *J. sista*, and their androconial clusters are scent patches. As noted under the species accounts, all but

TABLE 2. Ratio of length from forewing apex to base of vein 2A divided by length from base of vein 2A to terminus of vein 2A (Character 3). The gap criterion (see text) is exceeded between *J. flosculus* and *J. aurora* (t = 2.258, df = 14), between *J. armilla* and *J. malvina* (t = 2.872, df = 14), and between *J. rocena* and *J. leea* (t = 2.530, df = 14).

Taxon	Mean	SD	N	State
J. flosculus	0.852	0.0166	8	0
J. aurora	0.822	0.0334	8	1
J. armilla	0.817	0.0173	8	1
J. malvina	0.789	0.0222	8	2
J. sista	0.780	0.0155	8	2
J. rocena	0.768	0.0166	8	2
J. leea	0.752	0.0072	8	3
J. janthodonia	0.749	0.0202	8	3
J. janthina	0.745	0.0260	8	3
J. cydonia	0.732	0.0114	8	3

three *Janthecla* species have an androconial cluster on the dorsal forewing, but it differs in each species (except *J. sista* and *J. aurora*), and there is no unambiguous way to code it. As a result, we code only presence or absence of a ventral forewing scent patch.

Character 5. Ventral forewing (0) with black androconia (Fig. 8), (1) without black androconia (Fig. 2). Comment: Character state (0) occurs in eumaeines such as *"Thecla" falerina* Hewitson and *Arawacus leucogyna* (Felder & Felder) and state (1) in *Parrhasius m-album* (Boisduval & LeConte) and *Michaelus hecate* (Godman & Salvin) (Nicolay 1979).

Male genitalia. Janthecla species, except for J. rocena and J. malvina, had nearly identical male genitalia. Because cornuti seemed to vary interspecifically, we everted the vesica at the penis tip. Although the position of the cornuti on the everted vesica was invariant in Janthecla, it facilitated measurement of the ventral cornutus and may help solve homology problems among other eumaeines in the future.

Character 6. Ventro-lateral edge of tegumen with (0) no processes (Fig. 23), (1) with horizontal processes that lie above the valves (Figs. 24–26). Comment: The size and shape of the ventro-lateral processes vary greatly (Figs. 24–26), but most of this variation is intraspecific. Although many eumaeines have ventro-lateral processes of the tegumen that lie under the valves, such as *Pseudolycaena* (Clench 1964) and *Arcas* Swainson (Nicolay 1971b), the dorsal position of the processes in *Janthecla* is shared only with "*Thecla*" eronos Druce and "T." aepea Hewitson. These two species have nearly identical genitalia, and their processes are rectangular and massive in contrast to the delicate, triangular ones in *Janthecla*. The "T." eronos group shares no other character state with *Janthecla*, indicating a lack of close relationship with *Janthecla*, but appears to be a close relative of *Micandra* Schatz (Robbins 1987). On the basis of this evidence, we conclude that similarity in position of the processes in this group and in *Janthecla* is convergent.

Character 7. Elbow of gnathos (0) with a keel-shaped ridge (not illustrated), (1) without a keel-shaped ridge. Comment: Examples of state (0) among other eumaeines

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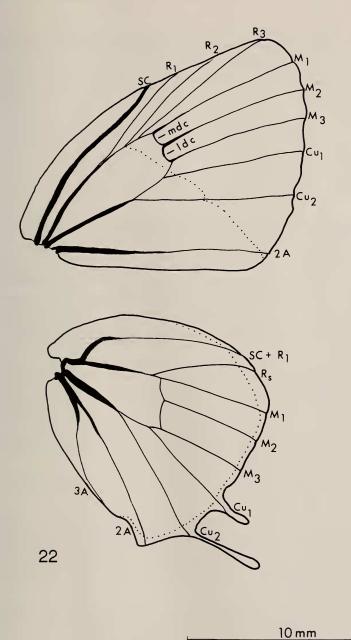


FIG. 22. Wing venation of J. leea with wing veins labelled.

Taxon	Mean	SD	N	State
I. janthodonia	0.050	0.0153	8	0
J. cydonia	0.067	0.0111	7	1
J. armilla	0.077	0.0157	8	1
J. leea	0.084	0.0191	8	1
J. janthina	0.091	0.0112	8	1
J. sista	0.101	0.0101	8	1
J. flosculus	0.215	0.0457	8	2
J. aurora	0.236	0.0270	8	2

TABLE 3. Width in mm of ventral cornutus (Character 10). The gap criterion (see text) is exceeded between *J. janthodonia* and *J. cydonia* (t = 2.459, df = 13) and between *J. sista* and *J. flosculus* (t = 6.857, df = 14).

are genera *Eumaeus* (Clench 1961) and *Symbiopsis* (Nicolay 1971a) and of state (1) are genera *Arcas* (Nicolay 1971b) and *Magnastigma* (Nicolay 1977).

Character 8. Setae on values (0) extend continuously to value tips (Figs. 23, 25, 26), (1) occur at the value tips and on the middle of the ventro-lateral surface of the values, but not in between (Fig. 24). Comment: State (1) occurs in no other eumaeines.

Character 9. Ventral cornutus (0) absent (Fig. 23), (1) shaped like an arrowhead (Fig. 24), (2) shaped like a tongue-depressor—the sides of the cornutus are parallel (Figs. 25, 26). Comment: Most eumaeines have 0-2 cornuti, but homology is unclear except among closely related species. Position of cornuti after being everted may be one solution to this problem.

Character 10. Average width of the ventral cornutus (0) <0.06 mm, (1) >0.06 mm and <0.16 mm, (2) >0.16 mm (Table 3). Comment: The ventral cornutus has small teeth at its ventro-distal end, and we measured width, after everting the vesica, just anterior to the teeth using a binocular microscope at $125 \times$, a drawing tube, and a digitizing pad. We coded *J. rocena* and *J. malvina* with a dash because the former lacks this cornutus and the latter has a cornutus differently shaped than the other species. Our gap criterion for recognizing different character states was significance at the 0.05 level using a two-tailed *t*-test, but as noted for Character 3, this coding does not mean that the differences were statistically significant.

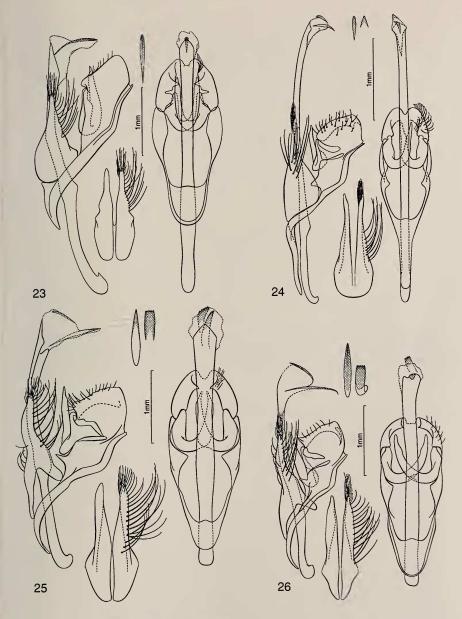
Female genitalia. As noted in the species accounts, we cannot distinguish females of some species.

Character 11. Ventral surfaces of the corpus bursae (0) directly below the dorsal surface attachment to the ductus bursae, (1) 0.25 mm or more posterior than the dorsal surface attachment to the ductus bursae (Figs. 27-29). Comment: Character state 1 characterizes *Janthecla*, although as noted, the ductus bursae of *J. malvina* curves sharply so that the points of attachment are ventral and dorsal, not posterior and anterior (Fig. 28).

Character 12. Anterior lamella postvaginalis (0) without dorsal and ventral longitudinal striations (Fig. 27), (1) with dorsal and ventral longitudinal striations (Figs. 28, 29). Comment: Character state 1, which occurs in all *Janthecla* species other than *J. rocena*, appears to be unique among Eumaeini.

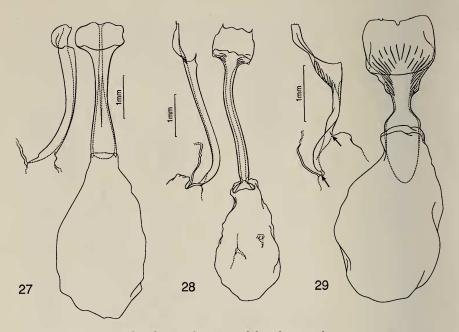
DISCUSSION

We derived a most parsimonious cladogram for *Janthecla* species (Fig. 30) using Hennig86 phylogenetic software (Farris 1988), but had



FICS. 23-26. Lateral, ventral (valves separate), and posterior (of cornuti) aspects of male genitalia. 23, J. rocena. 24, J. malvina. 25, J. janthina. 26, J. leea.

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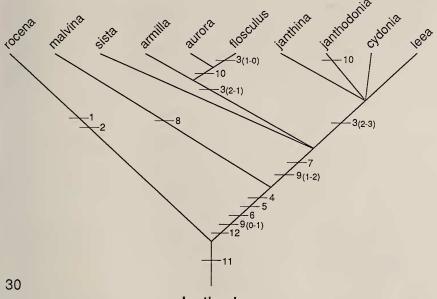


FIGS. 27-29. Lateral and ventral aspects of female genitalia. 27, J. rocena. 28, J. malvina. 29, J. leea. The arrow on the top of the lateral view shows where the ventral surface of the corpus bursae attaches to the ductus bursae whereas the one on the bottom shows where the dorsal surface of the corpus bursae attaches to the ductus bursae.

little success resolving relationships. Although no characters are homoplastic, there is a trichotomy and a quadrichotomy, and most nodes are supported by only one or two character state changes. Character numbers are indicated on the cladogram where changes in character state took place. Although these changes could be assigned in different, equally parsimonious ways, they support the same tree topology. Janthecla janthodonia, J. cydonia, J. leea, J. armilla, J. janthina, J. sista, J. aurora, and J. flosculus are morphologically very similar species, and we found few informative characters among them.

At the outset of this study, on the basis of geographical distributions (Figs. 6, 7), we hypothesized that J. janthodonia, J. cydonia, J. leea, and J. armilla formed a superspecies (a monophyletic group of nonoverlapping species) and that J. janthina, J. sista, J. aurora, and J. flosculus were a second superspecies. Although none of the species comprising either proposed superspecies are sympatric, the cladogram is inconsistent with our hypothesis.

Structure of the male foreleg has been used in the higher classification of the Eumaeini (Eliot 1973). Because the unusual male foreleg of J.



Janthecla

FIG. 30. Phylogeny of *Janthecla* species. Numbers designate where changes in character state occurred, as described in the text. For multi-state characters, the transformed states are added in parentheses: for example 3(2-1) is where state 2 of character 3 changed to state 1.

rocena (Fig. 21) does not occur in other Janthecla species, it appears to have evolved in the lineage leading only to it. Thus, it has no systematic importance at higher levels. This result is similar to that concerning the unusual male forelegs of *Trichonis hyacinthus* (Cramer), *Micandra platyptera* Felder & Felder, and "*Thecla*" myrtusa Hewitson (Robbins 1987).

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